THE ALPINE LIFE ZONE UNDER GLOBAL CHANGE

EL CAMBIO GLOBAL Y LOS ECOSISTEMAS DE ALTA MONTAÑA

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ABSTRACT

Nearly forty percent of mankind depend in one way or another on mountain ecosystems. Local ecosystem services are slope stability, water yield, agricultural products or recreational value. Continental scale influences include drinking water supply, ground water recharging, irrigation water, hydroelectric power, flood control, traffic routes etc. In this paper I review evidence of alpine ecosystem responses to global change. It is emphasized that soil conservation is the centerpiece of any consideration of sustainable land use in alpine terrain. Complete vegetation cover of high biological diversity is essential to protect soils and secure 'ecosystem services' in upland systems. It is illustrated that this is not necessarily in conflict with land use and that land use may even contribute to biological richness if appropriate management is adopted. Atmospheric influences such as increased nitrogen deposition, elevated CO_2 and climate warming induce subtle changes in alpine vegetation, the understanding of which requires experimental concepts which account for long term acclimation and organismic interaction. It is proposed that comparative approaches which cover interspecific variability and natural environmental gradients are most promising.

KEYWORDS: Altitude, biodiversity, climate, conservation, grazing, high elevation, land use, mountain ecology.

RESUMEN

Casi el 40% de la humanidad depende de alguna manera de los ecosistemas de montaña. Los "servicios ecosistémicos" locales incluyen la protección de las laderas, el rendimiento hídrico, los productos agrícolas y las oportunidades de recreo. Las influencias a escala continental incluyen el abastecimiento de agua potable y agua de riego, el recargamiento de acuíferos subterráneos, la generación de energía hidroeléctrica, la amortiguación de las fluctuaciones del caudal de los ríos, y las rutas de transporte. En este artículo, reviso las evidencias de las respuestas de los ecosistemas alpinos al cambio global. Se recalca que la conservación de los suelos es la pieza clave en cualquier consideración del uso sustentable de las tierras de montaña. Una cobertura completa de una vegetación diversa es esencial para proteger los suelos y asegurar los "servicios ecosistémicos" en los sistemas de montaña. Se demuestra que esta estrategia de conservación no entra necesariamente en conflicto con el uso productivo de la tierra, y que tal uso puede incluso potenciar la diversidad biológica si se adopta un manejo adecuado. Las influencias atmosféricas, tales como el aumento en la depositación de nitrógeno, niveles incrementados de CO_2 y el calentamiento global, pueden inducir cambios sutiles en la vegetación alpina. La comprensión de dichos cambios requiere modelos que den cuenta de la aclimatación a largo plazo, y de la interacción entre los organismos. Se propone que son promisorias las aproximaciones comparativas que abarquen la variación interespecífica y los gradientes ambientales naturales.

PALABRAS CLAVES: Altitud, biodiversidad, conservación, pastoreo, uso de la tierra, ecología de montaña.

INTRODUCTION

Lowlands depend on uplands and thereby the life of forty percent of the world's population is influenced by mountains, and 10% are directly

dependent (Messerli and Ives 1984, 1997). All advanced cultures of historical times were centered in climatically relatively dry areas, supported by water from remote mountain systems. Mesopotamia obtained its wealth from the Euphrates and Tigris rivers, draining the Anatolian highlands. Egypt's life line, the Nile, links to the uplands of equatorial Africa. Through the Ganges and other large river systems in Central and SE-Asia, the Himalayas

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supply India and south China. Modern societies, with an enormously increased human population, are even more dependent on such river systems and their recharging of ground water reservoirs. Also relatively "new" agro-technological developments in N-America, such as those in Arizona and California, are up to 100% dependent on the supply of irrigation water from mountains, in this case the Rocky Mountains and the Sierra Nevada of California. Most floods in lowlands have upland origins. The moisture storage capacity of uplands is a key factor in the rate of increase and height of floods. With altitudinally decreasing evapotranspiration and increasing precipitation, runoff can increase 5 to 10 fold as elevation increases from foothills to the upper alpine grassland belt (Fig. 1). This obviously calls for attention to steep alpine terrain and its soils in flood and land slide control.
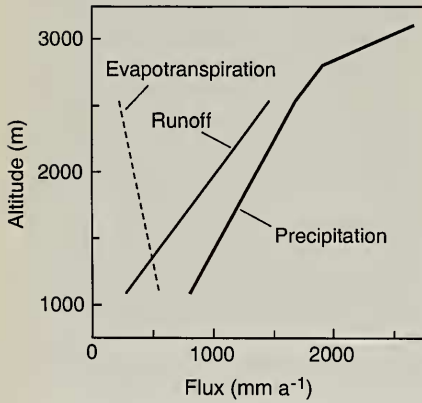

FIG. 1. One of the causes why alpine ecosystems are so fragile is the large surplus of water which passes through them in most places. The example shown here for the Alps is typical for many mountain systems. The combination of increasing precipitation and decreasing evapotranspiration cause large runoff, which requires stable soils and plant cover to resist erosion (from Körner et al. 1989b and Körner 1999).

With respect to direct local benefits, it is often overlooked that a substantial human population finds subsistence through mountain agriculture or -in modern times- tourism. These immediate benefits are essential to the welfare of countries like Austria, Switzerland or Nepal (e.g. Price 1997). Last but not least, mountain systems are barriers for transport, and the functioning of transport routes and corridors through the highlands is of great economic significance. The safety of these routs strongly depends on the stability of the upslope mountain terrain.

This review focusses on the alpine life zone, which is the region above the climatic high altitude treeline, irrespective of the actual presence of forest (Körner 1998). However many of the references and commentaries also relate to the treeline ecotone itself which is a zone of intensive land use in many parts of the world. Much of what is presented here is also relevant for man-made montane grassland which often replaces the montane forest.

For most people, including official land use statisticians, alpine vegetation ends where closed alpine grassland (mostly pastures) end. However, fragmented grasslands and open scree and fellfield vegetation reach much higher elevations. Biologically-rich plant communities are found at elevations substantially exceeding 4000-5000 m in the Himalayas and Andes and contribute to the overall consolidation of the high alpine landscape (e.g. Rawat and Pangtey 1987; Körner 1995, 1999). Most alpine plant species are long-lived and exhibit clonal growth, which makes them robust against disturbance and adverse seasons (Ram et al. 1988; Körner 1995). Root systems of native perennial alpine plants are more extensive than in lowland plants and tend to prevent soil and scree loosening and erosion (Körner et al. 1989a). Massive below-ground structures are crucial for ecosystem functioning at high elevation (Fig. 2).

What ever happens to the highlands will affect the lowlands through their intimate functional link. Hence, intact and ecologically stable uplands are of general interest to human welfare. I use the term 'stable' in the sense of functional integrity, persistent vegetation cover, intact soil profiles and minimum erosion, hence 'stable' is not to be misinterpreted as 'frozen' in a certain stage of internal ecosystem dynamics.

FIG. 2. Strong below-ground plant structures secure soils on steep slopes (*Carex curvula*, Swiss Alps, 2500 m).

There are few simple ecological rules for the stability and the risk potential in alpine and mountainous regions and their forelands:

(1) Mountain ecosystems and their dependent foothills are only as stable as the high altitude slopes and their soils are.
(2) On slopes soils are only stable with a stable vegetation.
(3) The stability of the vegetation depends on the presence of slow growing, deep rooted plants, which develop complete ground cover.
(4) Soils, once destroyed, cannot be replaced or repaired within a reasonable time frame, because it may take thousands of years for a soil profile and its typical plant cover to develop. At low elevation, erosion control by technology may be possible but this approach often fails in steep terrain above the alpine treeline.

Thus, vegetation and soils at and above treeline play a key role for the stability of life conditions in the mountains, as well as for the safety of water supply, flood control, traffic routes and recreational value for human populations living in the foothill zone. Given these links, there should be a wide interest in the current and future status of high altitude ecosystems, remote from the large metropolitan areas as they might be. In this contribution I discuss some of the threats alpine vegetation is facing today and will most likely face in the near future. Since these problems are not localized, but global, they are adequately addressed as global change issues.

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GLOBAL CHANGE IN HIGH MOUNTAINS

Life conditions for plants have always been in a state of flux and always will be, everywhere on the globe. High elevation vegetation is no exception in this respect (Barry 1990). However, these natural changes are commonly rather slow and of a largely physical nature. The current man-induced changes are rather rapid, include chemical influences (CO_2, soluble N, acid rain) as well as land surface management, causing unprecedented impacts (Messerli and Ives 1984, 1997; Price 1995). Intensification or the rapid abandonment of land use near the treeline are the most immediate dangers, followed by potential consequences of altered atmospheric composition. Climatic changes exceeding those seen in the recent past (warming, more intense rain events, reduced snow cover) may also become critical in places.

As mentioned above, the centerpiece of any consideration of global change impacts on alpine ecosystems is the stability of alpine soils. A persistent ground cover with intact root systems is thus the criterion by which the risk of all anthropogenic influences on high elevation ecosystems is to be rated. Below I will present a brief account of important global change risks for the alpine life zone.

Which global changes are most critical? Political discussions often center around those which are less critical, with distant causes, hence calling for little local action. Among those global threats, I will discuss consequences of air pollution by soluble nitrogen compounds and atmospheric CO_2 enrichment (both its direct effects on vegetation and indirect effects through possible climatic warming). However, I will first address the most critical global change component which has immediate and direct local influence, namely human land use at high elevations. No other component of global change has similar impact.

ALPINE LAND USE

The alpine zone may have been utilized by humans for as long as people lived in the foothills. Hunting and pasturing have influenced alpine vegetation for many thousands of years. "The man in the ice", a bronze age hunter or shepherd found with largely intact mountaineer outfit, released from retreating ice above 3000 m in the Central Alps of Tirol is a most obvious proof of man's active

presence in alpine environments, long before mass tourism (Eijgenraam and Anderson 1991; Spindler *et al.* 1995; Bortenschlager and Oeggl 1998). Remarkably, this ancient Tirolian was found in an area where contemporary farmers still herd their flocks from the South across the glaciers to summer pastures in the North of the main divide.

It is safe to assume that all alpine vegetation has undergone some influence of anthropogenic land use, except perhaps the most extreme elevations and inaccessible rock terraces. Populations of wild herbivores have been reduced by hunting (in the case of ibex in the Alps in fact eliminated during the 19th century) and were gradually replaced by seasonal pasturing with domestic livestock. Traditional man-made alpine pasture land near treeline is common in all mountainous regions with permanent settlements (all over Eurasia, parts of S-America) but is absent in areas with historically predominant nomadic life style (N-America, Australia).

It is largely because of these pasture lands that the Alps, the Carpathians, the Caucasus, the Hindukush and Himalayas have been praised by travelers for their colorful alpine mats. These pastures, with their wooden fences and stone walls, dwellings and shrines, drainage and irrigation systems, specific soil dynamics and very special flora also represent a unique cultural heritage. Traditional, and thus commonly sustainable management, only exceptionally leads to erosion. These traditional forms of land use are currently disappearing. For three reasons, measures to secure sustainable agriculture in traditional alpine pasture land near treeline are highly recommendable in many parts of the world:

• conserve biologically highly diverse, stable and also attractive plant communities,
• maintain a healthy, unpolluted food source for future generations,
• retain a millenial cultural heritage.

In pastures near treeline things can go wrong in three ways: (1) uncontrolled, non-traditional (i.e. patchy) grazing causing spot-impact under otherwise low stocking rates, (2) stocking beyond carrying capacity or introduction of excessively heavy cattle or (3) sudden abandonment of pastures. All three may affect soils and induce erosion or irreversible changes in ecosystem structure, such as shrub invasion. Soil destablization after abandonment has

to do with sudden occlusion of drainage systems (over-saturation of soils), and with turf-erosion caused by creeping late winter snow, frozen to rank grass growth. The risky transition period, back to self-sustainable ground cover, may take at least half a century (Cernusca 1978), but sensitivity varies a lot with slope and vegetation type (Gigon 1983). After abandonment, shrub and tree invasions rapidly alter ecosystems properties which slowly developed over millennia of manual work. A future reversal of this succession will most likely be unaffordable, hence the loss may be practically irreversible.

Adequate grazing regimes in alpine grassland can substantially improve hydroelectric catchment value through ensuring a short, dense and mechanically robust, but also biologically very rich, alpine turf. According to measurements and calculations by Körner et al. (1989b) the added value of appropriate pasturing in terms of clean water yielding may be in the order of 150 $ ha^{-1} f5 a^{-1} at current exchange rates. In contrast, inappropriate grazing in previously ungrazed, sensitive alpine vegetation negatively affects catchment value and enhances erosion (Costin 1958). This insight, i.e. the hydroelectric benefits of refraining from inadequate land use, contributed to the foundation of Kosciusko National Park in the Snowy Mountains of south-eastern Australia. The main impact of pasturing on alpine vegetation is caused by animal trampling rather than grazing as such. Late successional alpine turf with a dense root felt is rather robust, whereas low, prostrate dwarf shrub communities appear extremely sensitive in this respect (Körner 1980). The moister the soil, the steeper the slopes or the loser the substrate (e.g. volcanic ashes), the greater the vulnerability to trampling.

With adequate control, grazing may have no negative effects on alpine vegetation. In places, it may even improve local stability by favoring biological richness. Plant species richness generally tends to represent a sort of insurance for ecosystem integrity under stress or disturbance, because of the increased likelyhood of survival of some species or morphotypes (functional types) (Körner 1995). A recent study in the Swiss Alps revealed that 6 seasons of cattle exclosure (fence) from 'natural' alpine *Carex curvula* dominated grassland at 2500 m elevation (200-300 m above treeline) had unexpected negative effects: Total (life) above-ground phanerogam biomass at peak growing season (just before the first

cattle visits), was reduced in the fenced area by one fifth (Fig. 3), and there were clear indications of reduced abundance of rare forbs (Fig. 4).
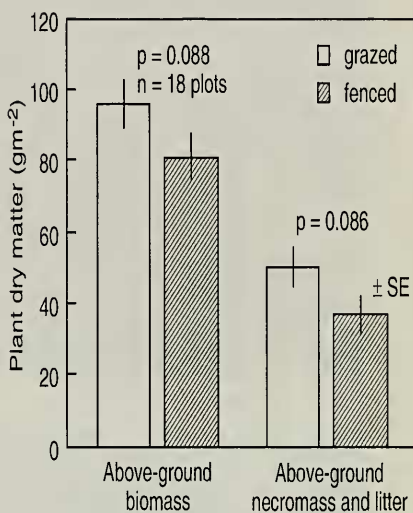

FIG. 3. Land use through grazing may impact alpine vegetation. However, adequate management of grazing may in fact have very positive effects on vigor, biodiversity and stability. Here an example for traditional, rather extensive midsummer cattle grazing. After 6 years of fencing a typical alpine grassland in the Swiss Alps at 2500 m altitude (300 m above treeline near Furka Pass), biomass and dead plant mass was reduced (unpublished data from S. Schneiter and Ch. Körner).

Hence, what is described in text books as one of the most typical, natural alpine grasslands, seems to benefit from sporadic cattle presence, both in terms of productivity and biodiversity. Dung deposition was found to create patch dynamics in this system with a statistical rotation time of ca. 50

years. On average 2% of the plant cover gets disturbed (largely killed) every year by dung deposits, but the surrounding vegetation gains in vigor. Overall the patch dynamics induced by dung deposition stimulates biological diversity. A positive biomass response to traditional alpine grazing was also observed in the Garhwal Himalaya (Sundriyal, 1992; Sundriyal and Joshi, 1992).
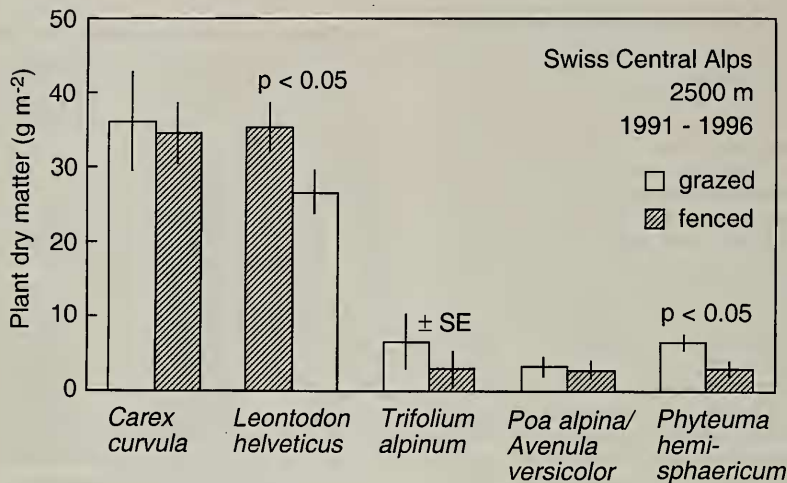

Fig. 4. Excluding moderate grazing in natural alpine grassland may cause biodiversity to drop. The abundance of some subdominant and rare species was reduced after six years of fencing (site and conditions as Fig. 2).

Ecologists should investigate and foster pasturing systems suitable for the lower alpine and upper montane zone, because choice of grazing regime makes a considerable difference for yield and pasture stability (Rikhari *et al.* 1992). The treeline ecotone is often the zone where pasturing is most intense, and where uncontrolled grazing in a laissez-faire mode can be disastrous. Without management (mobile fences, shepherds, salt provision sites), domestic animals tend to crowd in certain areas and stay away from others, causing patchy impact, which almost always leads to erosion. Herding corridors between pastures are the most vulnerable areas and need careful route selection and repair. Hence the question is not whether alpine pasturing is good or bad for alpine ecosystems, it is a question of how it is practiced.

A good example is the study by Ram (1992), who showed that the timing of biomass removal (early versus late season) in Himalayan pastures at 3600 m elevation was more important for yield and plant recovery than the intensity of biomass removal. Burning of alpine grassland, as is practised in areas with tall, unpalatable tussock grasses (e.g. tropical Andes, equatorial Africa, Mexico, New Zealand), removes a lot of total plant matter per unit land area, but the amount of green leaves may not change in the short term (Hofstede *et al.* 1995; Fig. 5). In the long term repeated burning mobilizes ecosystem nutrient pools and induces nutrient losses through seepage and runoff. It further negatively affects hydrology as was demonstrated for high elevation snow tussock by Mark and Rowley (1976) and Mark *et al.* (1980).

FIG. 5. Alpine tall grasslands are often burned to improve pasture quality, but long-term effects on hydrology, nutrient availability and biodiversity are negative (Nevado de Toluca, Mexico, 4000 m).

As an example of high altitude pasture management which could clearly be improved I would like to comment on a situation I have seen in the Langtang area of Nepal, which may be typical for other areas as well (Fig. 6 left). Similar conditions can be found in the Andes (Fig. 6 right). From visual impression, current grazing land on former forest land in the upper montane zone is reduced by approximately one third of the total deforested area due to scrub invasion (e.g. by *Berberis*). The remaining inter-scrub space is overgrazed. Those often thorny shrubs are apparently in expansion, while fire wood is carried to the uphill villages and tourist stations. It would seem logical to cut those bush lands, fuel small stoves with the wood-chips, save on transport, reduce forest wood cutting and improve pastures at the same time. My impression was that, apart from tradition, strong leather gloves are the only missing item, because a governmental stove progamme is under way albeit apparently poorly accepted, which is unfortunate. Perhaps the triple benefits mentioned above were not realized and communication was not effective. Ground cover of those pastures was far below 50%, whereas strictly shepherd-controlled sheep grazing on similar terrain in some parts of the Caucasus and the Alps led to very stable and productive, short and dense grass swards.

Fɪɢ. 6. Pastureland with yak in the Langtang Valley, Nepal 3200 m. Dense thorn scrub (*Berberis* etc.) diminishes pasture value.

Other, more localized, but rather severe forms of alpine land use are the construction and grading of ski runs and transport routes, intense summer tourism, hydroelectric installations and mining.

Rather sophisticated (and expensive) re-vegetation procedures may help in places to mitigate erosion problems (e.g. Urbanska and Schutz 1986; Grabherr 1995), but will not re-establish the stability of naturally evolved, deeply-rooted soil, and thus require sustained care. There is a lot of long term responsibility involved in the management and alteration of alpine terrain and its soils, given the rather low self-repair capacity and overall slow responses of alpine vegetation.

ATMOSPHERIC INFLUENCES

Although commonly far removed from urban agglomerations and industrial emissions, alpine ecosystems are affected by atmospheric pollution to variable degrees, and atmospheric CO_2 enrichment is a global phenomenon. Here I briefly comment on the three most important aspects of atmospheric change.

Soluble nitrogen deposition

It is well-established that many alpine regions in the northern hemisphere are currently receiving rates of soluble nitrogen deposition that are several times higher than pre-industrial levels (Bowman 1992; Williams et al. 1995), and alpine plants have been shown to be very responsive to N-addition (see Körner 1999), despite commonly high nutrient concentrations in their tissues (Körner 1989). More vigorously growing plants tend to be more receptive to this atmospheric fertilizer. Commonly such fast-growing species are not very robust against physical stress. Their increasing abundance under continuously enhanced N-availability could weaken the overall robustness of ecosystems. The comparatively low rates of N-deposition in the Rocky Mts. and the Sierra Nevada of California correspond to approximately one third of annual N-mineralisation in soils, but the rates reported for some parts of the Alps already exceed natural N-mineralisation. Late successional natural alpine grassland at 2500 m elevation in the Alps was found to double biomass when 40 kg of N per hectare were added during the growing season (Körner et al. 1997) and species number declined, with low stature species becoming overgrown.

Among all compounds deposited in alpine ecosystems, soluble nitrogen deserves greatest attention, because of the key role of nitrogen in plant metabolism and its immediate influence on plant growth. Acid rain may impose particularly severe changes in alpine aquatic systems (Psenner and Nickus 1986; Psenner and Schmidt 1992).

Atmospheric CO_2 enrichment

Elevated CO_2 has been expected to become most influential in plants at high elevations, because of the already reduced availability due to lower atmospheric pressure, and thus partial pressure. Results of gas exchange studies has indeed supported the idea of instantaneous (Billings et al. 1961; Mooney et al. 1966; Körner and Diemer 1987; Ward and Strain 1997) and prolonged (Körner and Diemer 1994; Diemer 1994) strongly positive effects of elevated CO_2 on alpine photosynthesis, in line with long term adjustments to life at high elevation as reflected in stable carbon isotope discrimination (Körner et al. 1991). However, results of four seasons of in situ simulation of a double-CO_2 atmosphere in alpine grassland in Switzerland did not support this view (Schäppi and Körner 1996; Körner et al. 1997; Fig. 7). Above-ground plant biomass remained completely unaffected and belowground effects were small but positive (+12%, P=0.09). These observations are in line with those by Tissue and Oechel (1987) for graminoid arctic tundra. CO_2-enrichment did, however, reveal some species specific responses (stimulation of more vigorous, currently very rare species), affected tissue quality of plants (less protein, more carbohydrates; Schäppi and Körner 1997), and did influence herbivore behaviour (significantly increased consumption by grasshoppers; see Körner et al. 1997). These more subtle effects may translate into significant ecosystem effects in the very long term. However, the net effect of CO_2-enrichment on the ecosystem C-balance approached zero after four seasons (see the synthesis in Körner et al. 1997). Overall the influences of doubled CO_2 are much smaller than those imposed by the application of amounts of soluble nitrogen, which are currently contained in the annual rainfall of many European lowland regions.

FIG. 7. CO_2-enrichment experiments in the Swiss Alps at 2500 m elevation. Elevated CO_2 did not stimulate plant growth, but affected plant quality and biodiversity, though only slightly, suggesting a very slow response (Körner *et al.* 1997).

Climatic warming

A most important feature of alpine plant life is "change" - rapid and small scale change of climatic and soil conditions. At first sight, the climatic changes predicted appear to be small compared to the natural spatial and temporal variation that alpine plants currently cope with. However, an overall warming and associated changes in precipitation patterns and snow cover will influence alpine vegetation in the long run (Guisan *et al.* 1995). Current predictions suggest that climatic change effects will be smallest in the tropics and strongest at high latitudes and are likely to be most pronounced in Western Europe and parts of Asia (Diaz and Bradley 1997). In the Alps, minimum temperatures have been predicted to increase much more than means (by 2K; Beniston *et al.* 1997). Winter minima

per se will have little effect on alpine plants, but if they affect snow cover they can become influential. However, there is evidence for the Swiss Alps that effects on snow cover generally diminish as elevation increases (Beniston 1997). The most sensitive areas are below treeline, not considered here. Evidence is accumulating that heavy rainfall events associated with warming (not necessarily extreme events) will become more frequent, which is likely to enhance erosion (e.g. Rebetez *et al.* 1997).

Predictions based on models assuming continuity of current plant-climate relationships and upslope migration tied to shifts in isotherm position (e.g. Ozenda and Borel 1990; Guisan *et al.* 1998) may overestimate change at the basis of vegetation belts (which are partly linked to soils and relief), but may underestimate effects on single species, the level at which migration appears to happen,

according to fossil records (e.g. Ammann 1995). Holten (1993) and Saetersdal and Birks (1997) suggested that species of narrow thermal ranges (often rare species) should be affected first. The conservative behaviour of large-scale vegetation boundaries is best evidenced by historical treeline position which does not seem to have directly tracked Holocene temperature fluctuations (Alps, Burga 1988; Andes, Lauer 1988).

One striking example that late successional plant communities may not respond to substantial climatic oscillations is the *Carex curvula* dominated alpine grassland in the Alps. This sedge resembles a clonal growth strategy and a physiognomy which is present in all mountains of the world. With its slow rhizomatous spreading of only 0.5 mm per year, this sedge forms tussock cohorts of particularly great age. Using DNA finger printing (PCR), it was possible to map genotype boundaries (Steinger *et al.* 1996) and estimate clone size and age. It emerged that single clones of this sedge must be several thousand years old, having persisted on the very same spot in the alpine landscape, while holocene temperatures passed through major deviations from todays climate (early medieval warm period, little ice age). Hence, such late successional plant assemblages may resist climatic changes over long periods.

The evidence that some alpine plants may still show significant response to climatic warming comes from two sides: simulation experiments with small open top greenhouses such as the ones used in the International Tundra Experiment (ITEX; e.g. Henry and Molau 1997), and re-visitation of pioneer habitats of extremely high elevations (Hofer 1992; Gottfried *et al.* 1994; Grabherr and Pauli 1994). The latter authors calculated mean 10-year up-slope movement of plant species of 1 to 4 m in elevation for various mountain tops in the Alps. They thus confirmed trends already suggested by Braun-Blanquet (1956), who noted increased plant species presence above 3000 m elevation in years 1947-1955 as compared to the years 1812-1835.

Temperature increases in the range of interest here (1-3 °K) are not necessarily enhancing plant metabolism, because cold-climate plants commonly adjust their respiration to prevailing temperatures (Criddle *et al.* 1994; Larigauderie and Körner 1995; Arnone and Körner 1997), though perhaps not completely in all cases. It has been known for over 60 years that plant tissues from arctic environments exhibit respiratory losses similar to those in tropical forest plants when both are studied under their real life conditions (for reference see Körner and Larcher 1988; Körner 1999). However we know little about the time constants of thermal acclimation, in particular the differential responses of above and below ground organs that are exposed to widely contrasting thermal conditions. In the temperate zone, assimilation and release of CO_2 by plants, although of key importance to plant growth, are the least likely bottleneck where climate warming would become effective. From what is known today it seems that formative (growth) processes *per se* are the most sensitive component of plant growth in cold climates (Körner *et al.* 1989c; Körner 1999).

The most common observation during *in situ* warming experiments in temperate and subarctic latitudes (e.g. ITEX, International Tundra Experiment, Henry and Molau 1997) was little effect on vegetative growth (biomass production), but substantial phenological acceleration in both arctic and alpine areas (e.g. earlier flowering; Wookey *et al.* 1994; Havström *et al.* 1995; Alatalo and Totland 1997; Stenström *et al.* 1997; Suzuki and Kudo 1997; Molau 1997; Stenström and Jonsdottir 1997; tests for *Carex, Cassiope, Saxifraga, Silene*). This is in line with conclusions by Prock and Körner (1996) that early season development of cold climate plants is opportunistic, while late season phenology is deterministic (photoperiod controlled). Hence, climatic warming will largely affect early season development, the key to which is the possibility of earlier snow melt (Guisan *et al.* 1995, 1998; Guisan 1996). In regions with potential topsoil desiccation and thus drought-induced nutrient shortage in midsummer, accelerated snow melt may, however, have negative effects (Walker *et al.* 1995). As a plausible alternative to bulk up-slope migration, Grabherr *et al.* (1995) has suggested local niche filling and re-arrangements in vegetation mosaics, driven by patterns of snow distribution and microclimate.

The steep thermal gradients over short distances observed in alpine terrain provide an unprecedented opportunity for testing long-term effects of contrasting temperatures in an otherwise similar environment (Fig. 8). These "natural experiments" have the great advantage that they have been run for periods longer than any funding

period in experimental ecology ever will. From physiology to soil studies such gradients have a lot to offer in plant, animal and microbial sciences. One can easily find microhabitats with 2-3 K difference in mean temperature (what global circulation models predict for a $2x$ CO_2 world), hence replication is theoretically unlimited. It is surprising how little use

of such natural experiments had been made in the past. An excellent example of the power of such "experiments" are the studies on reproductive biology at different slope aspects in the high Andes by Kalin-Arroyo et al. (1981), Arroyo et al. (1982), and Arroyo et al. (1985). This is certainly a field to be developed, with no costs for 'treatments'.
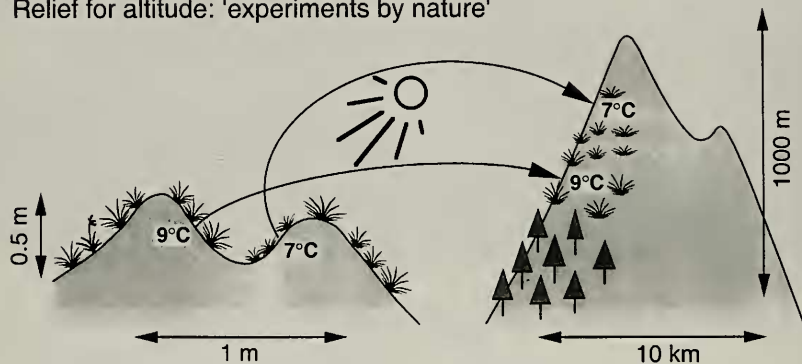

FIG. 8. Global warming may impose accelerated metabolism and plant migration. The alpine landscape with its mosaic of microhabitats offers a multitude of "natural experiments" which can be used to study the effect of temperature on plant life without expensive growth facilities. Relief driven thermal gradients may serve as models for large altitudinal or latitudinal gradients in climate.

The comparative approach is vital to an understanding of alpine plant life. It is important that various ways of comparing plants of different elevations are distinguished (Fig. 9). Specialist plants, exclusively found at high altitudes, will more likely reflect a high degree of 'adaptation' in their characteristics, and hence can be expected to behave in a more typically 'alpine' manner, than plants which recently radiated from their lower elevation centers of distribution to high elevation outposts. However, a single specialist species with a narrow high altitude range is still a weak indicator of life zone specific behaviour, because there is a large structural and functional diversity among plant species

even at highest elevations (Körner and Larcher 1988; Körner 1989; Körner et al. 1989a; Körner 1991). It is the habitat-altitude-specific community of species, and the relative frequency of traits among those species, that bear the most reliable message with respect to life zone specific adaptive responses (Körner 1991). Provenances or ecotypes of single species from a wide altitudinal range, extending far beyond the zone of their greatest abundance, have the advantage of closer taxonomic relatedness, but may be 'Jacks of all trades'. Hence are less likely to bear most characteristic features of the highest life zone of plants.
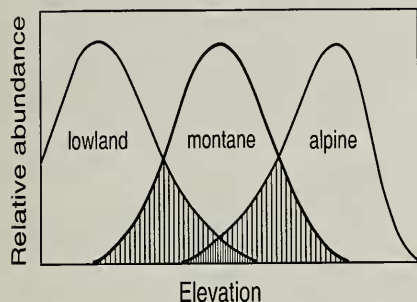
Fig. 9. Functional ecology of alpine plants depends on comparative studies. This diagram illustrates three typical ranges of plant species distribution along an elevational gradient. It is important to distinguish responses of wide ranging species of otherwise medium elevational dominance (middle curve) from those between specialists from contrasting elevations (left and right curve). It also matters whether species are tested across their own range or whether different species are compared which have contrasting ranges of distribution. The latter often is more relevant, but requires broad sampling to cover intra-community variability, hence is more laborious (from Körner 1999).

As was discussed above, alpine plant responses to environmental changes will strongly depend on species and growth conditions. Quite different responses may be seen on fertile compared to infertile substrates. It therefore seems, that the safest approaches are those which consider plants in natural soil and account for interspecific differences as well as interactions, which have been shown to be significant (e.g. Sundriyal and Josill 1992). *In situ* research commonly leads to greater variability in experimental results, but this is the price to be paid for greater relevance. Greater sample sizes and more work are commonly required to meet these criteria of realism, hence costs of this sort of research are often higher than in standardized laboratory tests. In the ideal case plants are studied *in situ* as well as under controlled conditions, which includes their responses under conditions of natural

microbial rhizosphere coupling, possibly the most critical aspect of experimental global change research (Körner 1996; Niklaus and Körner 1996; Niklaus 1998).

CONCLUSIONS

In summary, rising temperatures, longer growth seasons, increased nitrogen supply and enhanced CO_2 concentrations alone or in combination will reduce some of those constraints dominating alpine plant life. 'Lessening' these 'limitations' will open alpine terrain for migrations from lower elevations and will also create pressure for upward migration of alpine species. Actual migration will always depend strongly on migration corridors and whether mountains provide high enough escapes with suitable growth substrates. Whether rates of migrations will track current rapid changes seems doubtful (Körner 1994). Most alpine species are capable of some form of clonal, rather slow mode of propagation and thus may retain sites irrespective of such climatic variation as was illustrated for clones of *Carex curvula* which have persisted several thousand years on the very same spot in the Alps while climate had undergone substantial variation. Obligatory seeders and alpine 'ruderals', restricted to open high elevation terrain, are thus the most likely components of the alpine flora to exhibit fast responses. Late successional, closed vegetation will change very slowly if at all (with N-deposition bearing the greatest influence).

Compared to these atmospheric changes, the direct human influences which are discussed are much more severe and immediate. The current rapid and worldwide detoriation of the lower alpine vegetation belts and traditional pasture land near treeline calls for rapid intervention. In the European Alps large parts of millennia old, stable pastures became abandoned for economic reasons, and their famous biological richness as well as their potential as a sustainable food source is about to be lost. The transition to forest often takes less than 50 years, certainly less than 100 years and is largely irreversible and often associated with unstable intermediate stages which are sensitive to moisture loading (slope gliding) and snow pressure (e.g. Cernusca 1978; Tappeiner and Cernusca 1998). On the other hand, the world witnesses massive

overgrazing and destructive use of fire and soil erosion in large parts of the Andes, the Afro-alpine zone and the Himalayas (Messerli and Ives 1997; Körner 1999), with severe hydrological and safety implications for settlements and traffic routes. I discussed general principles of sustainable use of such highlands, and it seems the main problem is the loss of responsibility and tradition of controlled pasturing that guaranteed long-term intergrity of these alpine rangelands.

Finally, wild plants inhabiting high alpine terrain have a great potential for bio-monitoring atmospheric influences on a global scale, because such cold climate wilderness habitats are unique in occurring at all latitudes (Körner 1992, 1995, 1999). Hence, well-documented historic research sites in alpine areas represent invaluable reference points for global change research. Re-visiting such sites for which historical inventories of plants or animals are available, is one of the most powerful tools to document vegetation change at high elevation. If done at a global scale by many teams such re-assessments of alpine biodiversity will allow us to separate regional from global trends imposed by global change.

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